

Structure of pelagic food webs in low-alkalinity lakes – forested and alpine catchments

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Abstract

Pelagic food webs in 15 lakes from European mountains were investigated during ice-free seasons. Eight lakes were acidified: pH below 6, alkalinity below 20 $\mu\text{eq l}^{-1}$. The range of total phosphorus (TP) in all lakes was 0.5–12.5 $\mu\text{g l}^{-1}$ without relation to pH. In alpine catchments, the only lakes with TP above 5 $\mu\text{g l}^{-1}$ were Starolesnianské pleso (Slovak Tatra, catchment with high soil cover), and Jörisee III (Swiss Alps, glacier inflow). Bacteria (BAC) were more important in pelagic food webs, both in terms of biomass and of activities, than in lowland lakes and reservoirs. Heterotrophic protozoans were mostly scarce. Total pelagic biomass (Tbi) was directly correlated with TP concentration (log/log). Total heterotrophic microbial biomass (THMi) reached 8.1 to 170 $\mu\text{g l}^{-1}$ C, i.e. 5 to 90% of Tbi. The highest THMi were found in Bohemian Forest. In Starolesnianské pleso the highest phytoplankton biomass (PHY) and PHY/THMi ratio were observed. The lowest zooplankton (ZOO) to PHY and ZOO/Tbi ratios occurred in the lakes of Bohemian Forest and of Tatra Mts. The percentage of exudation in total primary production was higher at low total production (20 – 90 in alpine lakes).

Key words: pelagic biomass, heterotrophic/autotrophic, bacteria, low-alkalinity lakes

Introduction

Mountain lakes, remote and often hardly accessible, are oligotrophic, though they might be loaded by nutrients (N oxides, ammonia) from the air. They are exposed to harsh abiotic conditions, long ice and snow cover, sudden fluctuations of rain and flow. In the areas with crystalline bedrock, they are sensitive to acidification. Nevertheless, biological in-lake processes might significantly change the chemistry of rainwater loaded to their catchment.

Pelagic food webs of mountain lakes are often rather simple compared to lowland lakes. Fish might be absent or scarce and sometimes not able to reproduce in the lake. Fish species present are not planktivorous, though at low food resources omnivory is to be expected. Heterotrophic component of plankton is more important and should not be neglected (FOTT & al. 1992, STRAŠKRABOVÁ & ŠIMEK 1993).

In clear-water mountain lakes (not dystrophic) of European mountains, phosphorus is expected to be a major limiting nutrient since nitrogen is supplied from the atmosphere. In alpine catchments, external loading by organic carbon is low (BARON & al. 1991) and primary

production is a significant source of organic carbon. So a relation of pelagic biomass to phosphorus is to be expected. A lot of data from meso- to eutrophic lakes were summarized to find chlorophyll (or primary production or phytoplankton biomass) to P relations and to predict or to control eutrophication (VOLLENWEIDER & KERÉKES 1982). Models for predicting phytoplankton and zooplankton biomasses in meso- to eutrophic lakes under a different P loading were constructed (ANDERSEN 1997) presuming that herbivores are related to primary producers. Bacteria have not been considered as a part of pelagic biomass, though they might be important sources or sinks for nutrients (STRAŠKRABOVÁ & al. 1999b) utilizing both allochthonous and autochthonous production. A scarcity of zooplankton and a simplicity of pelagic food webs with an important bacterial component have been documented in the lakes of Tatra Mts and Bohemian Forest (FOTT & al. 1992, FOTT & al. 1994, VRBA & al. 1996).

In the present study we have evaluated a unique set of quantitative data on pelagic biomass including bacteria and protozoans from low-alkalinity lakes in various European mountains. We have tried to elucidate relations between total pelagic biomass and phosphorus in oligotrophic and ultraoligotrophic lakes and the interrelations between particular components of plankton with the special emphasis on microbes. We hypothesize that towards decreasing trophicity, the relative importance of bacterial component increases, which is connected with the following phenomena: (i) with decreasing trophicity and primary production the percentage of extracellular release (readily utilizable by bacteria) was found to increase (STRAŠKRABOVÁ & al. 1999a), (ii) with decreasing trophicity the ratio of zooplankton to phytoplankton biomass decreases especially in acidified lakes.

Material and methods

Lakes

15 lakes in European mountain ridges were investigated (Table 1). All the lakes are situated on crystalline bedrock, they are of glacial origin, without permanent inhabitants and without any considerable anthropogenic pollution in their catchments (except of air pollution). They are head water lakes, except of the Norwegian lake Øvre Neådalsvatn, which is the second lake. Geographic location of the lakes covers a rather broad range, from 37°03' N to 67°55' N and from 3°13' W to 32°30' E (from La Caldera to Chuna), and from 420 to 3050 m a.s.l. of elevation (from the most northeast lake Chuna to the most southwest La Caldera). Except of the three lakes in Bohemian Forest (Šumava, CZ) in forested catchments, all the other lakes are in alpine catchments above a local timber line. Among alpine lakes, Starolesnianské and Gossenköllesee have a considerable soil cover in their catchments. The lakes differ in morphometry as well as in hydrology: water residence time is below 35 days in Øvre Neådalsvatn, Paione Superiore and Długi Staw, whereas it is 100 to 350 days in the others. Jörisee is fed by the inflow from glacier. Lakes in Bohemian Forest and in Tatra Mts receive the highest nitrogen loading (deposition above 0.7 g m⁻²y⁻¹ N), whereas Øvre Neådalsvatn received less than 0.35 g m⁻²y⁻¹ N. Acidification is most pronounced in the lakes of Bohemian Forest (pH 5 and lower), and less severe (pH between 5–6) in Starolesnianské, Długi Staw, Paione Superiore, Lochnagar and Stavsvatn. Attempts to introduce fish into the originally fishless lakes have occurred frequently, but recently, fish (brown trout) were found to survive only in 7 lakes: Øvre Neådalsvatn, Chuna, Redó, Jörisee, Gossenköllesee, and without in-lake reproduction in Stavsvatn and Lochnagar. Data on chemistry and atmospheric loading of lakes were reported by THE MOLAR WATER CHEMISTRY GROUP (1999), VRBA & al. (1996), KOPÁČEK & HEJZLAR (1998).

Table 1. – Location of lakes, basic data on morphometry and lake water chemistry (surface layer, average values for the period studied), chemical data by KOPÁČEK (unpubl.) and by THE MOLAR CHEMISTRY GROUP (1999).

Lake	District (country)	Altitude m a.s.l.	Area ha	Max. depth m	Volume m ³ 10 ⁶	pH	Alkalinity µeq l ⁻¹	Total N µg l ⁻¹
Lochnagar	Scotland (UK)	785	9.8	24.0	0.82	5.3	7.5	304
Stavsvatn	South Norway (N)	1053	40.0	17.0	2.50	5.9	18.0	181
Øvre Neådalsvatn	Central Norway (N)	728	50.0	18.0	1.95	6.2	32.0	65
Chuna ozero	Kola peninsula (RU)	420	12.5	18.0	1.25	6.2	20.0	96
La Caldera	Sierra-Nevada (E)	3050	2.3	11.3	0.11	8.1	343.0	249
Estany Redó	Pyrenees (E)	2240	24.0	73.0	7.75	6.4	47.0	251
Jörisee III	Swiss Alps (CH)	2490	57.8	21.8	0.60	7.0	118.0	1000
Lago Patone Superiore	Central Alps (I)	2269	1.4	11.5	0.07	5.8	7.5	>336
Gossenköllesee	Tyrol Alps (A)	2417	1.7	9.9	0.08	6.8	86.0	410
Starolesnianské pleso	Tatra (SK)	2000	0.7	4.1	0.01	5.0	-3.0	394
Nížné Terianské pleso	Tatra (SK)	1941	4.8	44.4	0.89	6.5	77.0	616
Długi staw	Tatra (PL)	1783	1.6	10.6	0.08	5.6	5.0	603
Plešné jezero	Bohemian Forest (CZ)	1090	7.5	18.0	0.62	5.0	10.0	840
Prášilské jezero	Bohemian Forest (CZ)	1079	3.7	15.0	0.27	5.0	-1.0	790
Čertovo jezero	Bohemian Forest (CZ)	1028	10.3	36.0	1.85	4.8	1.0	870

Table 2. – Description of sampling – *data partly elaborated by other authors, **all data elaborated by other authors.

Lake	Years of study (ice-free seasons)	Number of layers per sampling	Total number of samplings
Lochnagar	1996, 1997	3	6
Stavsvatn	1996, 1997	3	7
Øvre Neådalsvatn	1996, 1997	3 – 5	7
Chuna ozero*	1996, 1997	3	6
La Caldera**	1996, 1997	4	10
Estany Redó**	1996, 1997	4	11
Jörisee III*	1996, 1997	3	8
Lago Paione Superiore*	1996, 1997	2	9
Gossenköllesee*	1996, 1997	5	8
Starolesnianské pleso	1996, 1997	1 – 2	11
Nižné Terianské pleso	1996, 1997	3	10
Długi staw*	1996, 1997	2 – 4	7
Plešné jezero	1997, 1998	2 – 5	13
Prášilské jezero	1997, 1998	2 – 5	10
Čertovo jezero	1997, 1998	2 – 5	12

Sampling

Samples were taken at the deepest site in the lake during two ice-free periods, at least three times each season, in one to five layers, according to the lake maximum depth (see Table 2). A vertical sampler (van Dorn-type) was used for sampling bacteria, heterotrophic nanoflagellates, ciliates, phytoplankton and small (<40µm) zooplankton. A quantitative net (200 µm mesh size) of the Apstein type was used for large zooplankton.

Primary production, exudation and utilization by bacteria was measured in three lakes (Øvre Neådalsvatn, Starolesnianské pleso and Długi Staw) during expeditions in 1996 and 1997 and regularly in the three lakes of Bohemian Forest during 1997 and 1998.

The sampling procedure and the elaboration of samples followed the unified protocols used in MOLAR (EC 4th framework programme) project (details in STRASKRABOVÁ & al. 1999a).

Bacteria (BAC)

Samples preserved by formaldehyde were filtered through polycarbonate filters (0.2 µm pores), stained by DAPI (PORTER & FEIG 1980) and counted using an epifluorescent microscope. Cells were sized by semiautomatic image analysis system and volumes calculated according to PSENNER (1993). In cases when filamentous bacteria prevailed, total length of filaments was assessed by the line-intercept method (NEWMAN 1966, NEDOMA & al. 2000). Bacterial carbon biomass was derived from the allometric cell volume/cell C content ratio reported by NORLAND (1993).

Heterotrophic flagellates (HNF)

Formaldehyde fixed samples were concentrated on 1 µm pore size black polycarbonate filters, stained with DAPI and counted in an epifluorescent microscope (each flagellated individual checked for the presence of autofluorescing plastids). Cell lengths and widths were

measured with a calibrated ocular micrometer and volumes calculated as prolate spheroids. Cell volumes were converted to carbon by a factor of $220 \text{ fg C } \mu\text{m}^{-3}$ (BORSHEIM & BRATBACK 1987).

Ciliates (CIL)

Samples fixed with a Lugol's solution (VOLLENWEIDER 1974) were sedimented and assessed in sedimentation chambers under an inverted microscope. Cell lengths and widths were measured and volumes calculated as prolated spheroids. After correction for shrinkage in Lugol by a factor of 1.4 (MÜLLER & GELLER 1993), volume biomass was converted to carbon by a factor of $140 \text{ fg } \mu\text{m}^{-3}$ (PUTT & STOECKER 1989).

Phytoplankton (PHY)

Lugol preserved samples were concentrated by sedimentation and assessed in sedimentation chambers under an inverted microscope. Cells were determined, counted and cell dimensions measured using an electronic caliper connected to a PC (LEGNER & SPRULES 1993). Individual cell volumes of the main species were calculated as volumes of geometrical bodies approximating shapes of the cells. Conversion factor of 0.2 was used to convert volume biomass (mm^3) to carbon (mg). The factor was checked in the culture of *Rhodomonas* sp., cultivated in a P-limited chemostat (see STRAŠKRABOVÁ & al. 1999a).

Zooplankton (ZOO)

Formaldehyde preserved concentrated samples were washed on a $40 \mu\text{m}$ sieve before elaboration and counted microscopically in the chambers of Sedgwick-Rafter or Utermöhl type. The biovolume of rotifers was estimated according to RUTTNER-KOLISKO (1977), volumes of species, which contract after preservation, were calculated as ellipsoids. Biovolume was converted to carbon assuming dry-to-wet weight ratio 0.1 (PACE & ORCUTT 1981) and carbon-to-dry weight ratio of 0.5. A similar procedure was used for nauplii, volumes were calculated according to MANCA & COMOLI (1999). The biomass of other crustaceans was estimated from their length-dry weight relationships (McCAULEY 1984), assuming carbon as 50 % of dry mass.

Primary production and exudation

The layers 0.5 m and $2\times$ Secchi disc depth were sampled plus another 1 to 3 layers between (according to the depth of lake). From the same layers samples for inorganic carbon (DIC) were taken. From each layer, two dark and two light quartz glass bottles (200 ml) were filled and ^{14}C -bicarbonate (0.5 MBq in $50\text{--}200 \mu\text{l}$) added to each. Exposition was at the sampling depths for 2–3 hours and then the samples were immediately elaborated.

A 1 ml subsample from each bottle was transferred into a vial with α -phenethylamine for the determination of total activity. A defined volume of a sample was then filtered through an „algal“ filter ($1 \mu\text{m}$ porosity Nuclepore, according to the size of prevalent algae), the filter placed into the scintillation vial (A) and the filtrate collected. 10 ml of filtrate was transferred into the scintillation vial (B+C), acidified by HCl, left opened overnight and then neutralized by NaOH. The rest of filtrate was preserved by formaldehyde and later filtered through $0.2 \mu\text{m}$ filter to collect bacteria (B). Radioactivity was measured by liquid scintillation. Values from light bottles were corrected for dark bottle values. DIC was determined by carbon analyzer or estimated from pH and alkalinity (using GRAN titration) after correcting for temperature and ionic strength. Carbon production in all fractions was calculated from the ratio of total activity added and DIC, corrected for isotope discrimination of phytoplankton (VOLLENWEIDER 1974).

Values are interpreted as follows: (A+B+C) = gross primary production (total production), (A) = net primary production (algal cell production), (B+C) = extracellular production (exudation), (B) = part of extracellular production incorporated by bacteria during the exposure. Bacterial respiration of phytoplankton exudates used during the exposition was neglected. In samples with large filamentous bacteria as well as in samples with autotrophic picoplankton, the size separation between bacteria and phytoplankton is not possible and only (A+B) = phytoplankton cellular production plus part of extracellular production used by bacteria, and (C) = extracellular production not used by bacteria, could be distinguished.

Results

For each lake, average biomasses (expressed as μg carbon per volume) of particular plankton components – bacteria, heterotrophic nanoflagellates, ciliates, phytoplankton and small zooplankton – were calculated after pooling the data from all sampling depths and all sampling dates per two ice-free seasons. Table 3 shows the average biomasses of total heterotrophic microbes (bacteria plus heterotrophic nanoflagellates plus ciliates), of heterotrophic nanoflagellates, of ciliates, of total zooplankton, of total phytoplankton as well as the total pelagic biomass. Lakes are ordered according to the total heterotrophic microbial biomasses, starting with the highest values. The highest heterotrophic microbial biomasses as well as the highest total pelagic biomasses were found in the lakes of Bohemian Forest (forested catchments) and in Starolesnianské pleso (a lake in alpine zone, but with a high proportion of soil in its catchment). Heterotrophic protists were scarce in many lakes and they did not surpass 5% of total heterotrophic biomass in 6 lakes: in the lakes of Bohemian Forest and in Lochnagar, Długi Staw, and Jörisee III. Autotrophic picoplankton was very

Table 3. – Data on structure of pelagic biomass expressed in carbon ($\mu\text{g l}^{-1} \text{C}$) – average values of all sampled layers and all samplings per lake. THMi – total heterotrophic microbial biomass (bacteria, HNF and CIL), HNF – heterotrophic nanoflagellates, CIL – ciliates, ZOO – zooplankton, PHY – phytoplankton, Tbi – total pelagic biomass (THMi+ZOO+PHY), * values from references: CALLIERI & BERTONI (1999), FELIP & al. (1999), FOIT & al. (1999), HINDER & al. (1999a), HINDER & al. (1999b), PUGNETTI & BETTINETTI (1999), STRASKRAHOVA & al. (1998), WILLE & al (1999).

Lake	THMi	HNF	CIL	ZOO	PHY	Tbi
Plešné jezero	169.0	2.80	0.60	0.10	168.5	338.4
Čertovo jezero	142.4	0.05	0.40	0.01	76.4	218.8
Prášilské jezero	75.6	0.10	0.50	53.70	228.8	358.1
Starolesnianské pleso	51.4	14.60	4.50	4.73	880.0	936.0
Lago Paione Superiore	29.3	5.22	*2.21	*51.30	*12.0	92.5
Lochnagar	28.4	1.85	0.07	29.30	10.8	68.5
Stavsvatn	20.5	1.85	0.20	29.30	46.7	114.0
Długi staw	18.5	0.29	*0.06	<0.01	2.0	20.5
Jörisee III	17.9	2.93	<0.01	16.60	14.8	49.3
Gossenköllesee	*16.1	*5.99	*0.21	27.20	84.9	128.0
Nižné Terianské pleso	15.5	0.69	1.05	2.81	25.4	43.7
Éstany Redó	*11.9	*4.15	*4.04	*5.50	*34.1	*51.4
Øvre Neådalsvatn	11.8	0.76	0.33	7.25	10.9	29.9
Chuna ozero	8.1	0.59	0.10	*64.10	*44.1	116.0
La Caldera	*6.9	*0.11	*2.82	*21.40	*42.1	*70.4

scarce or absent in most lakes and it was found regularly only in Lochnagar and Jörisee III.

The proportion of bacteria in the total pelagic biomass was 30 to 89 % in 7 lakes: Plešné, Čertovo, Lochnagar, Długi Staw, Jörisee III, Nižné Terianské and Øvre Neådalsvatn. In five lakes (Starolesnianské, Gossenköllesee, Estany Redó, Chuna, La Caldera), bacterial share in total biomass was very low – 3.5 to 8%.

Total pelagic biomasses (T_{Bi}) were significantly correlated ($P < 0.001$) with total phosphorus concentrations (TP) in log/log scale (Fig. 1). Phosphorus concentrations were referred according to THE MOLAR WATER CHEMISTRY GROUP (1999), they were analyzed in surface layers and averaged per the whole two-year sampling period, including several data from winter. They might be considered as characteristic values indicating the trophic status of particular lakes. The only exception from T_{Bi}/TP relationship was the lake Jörisee III (not included in correlation) where at P concentration comparable with that in the Bohemian Forest lakes both the total pelagic biomass, phytoplankton biomass and heterotrophic microbial biomass reached 7×, 12× and 10× lower values, respectively (compare Table 3).

Similarly, a significant correlation ($P < 0.001$, $r = 0.82$, $n = 14$) was found between phytoplankton biomass and TP (again with the exclusion of Jörisee III). The log/log regression has not only a lower intercept (0.52 compared to 0.88), but also a lower slope (0.59 compared to 0.78) than the log/log regression of total pelagic biomass vs P shown in Fig. 1.

In Fig. 2, both the biomasses of phytoplankton and zooplankton (not transformed to logs) are plotted vs log P. Unlike phytoplankton, the zooplankton biomass did not correspond either to total P or to total pelagic biomass. In several lakes, the zooplankton biomass is extremely low compared to phytoplankton biomass, like in the three lakes of Bohemian

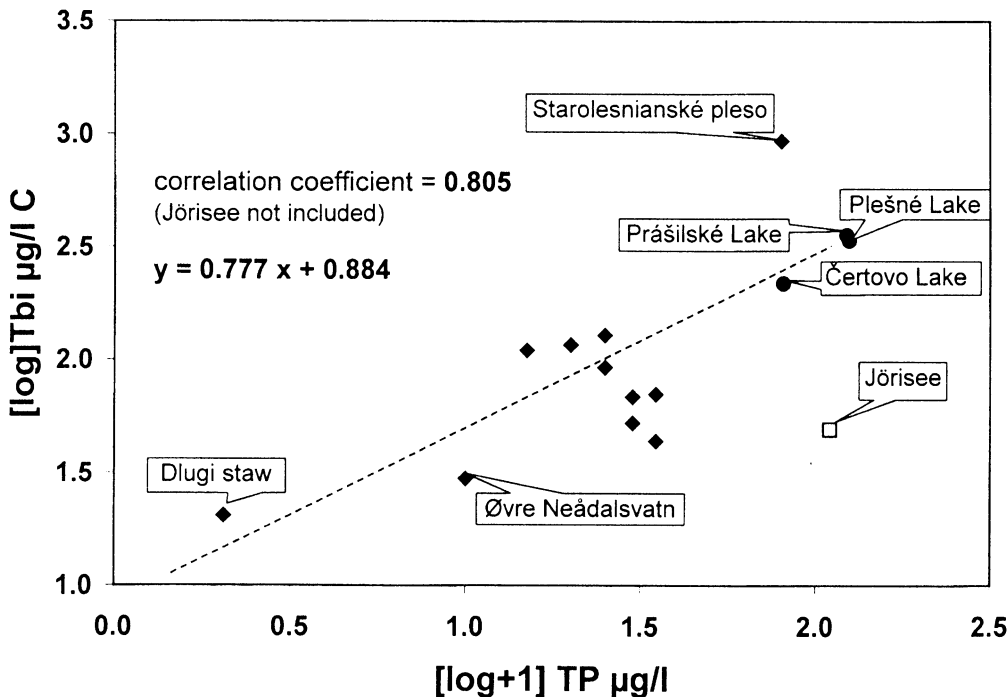


Fig. 1 – Total pelagic biomass vs. total P, log/log plot, averages.

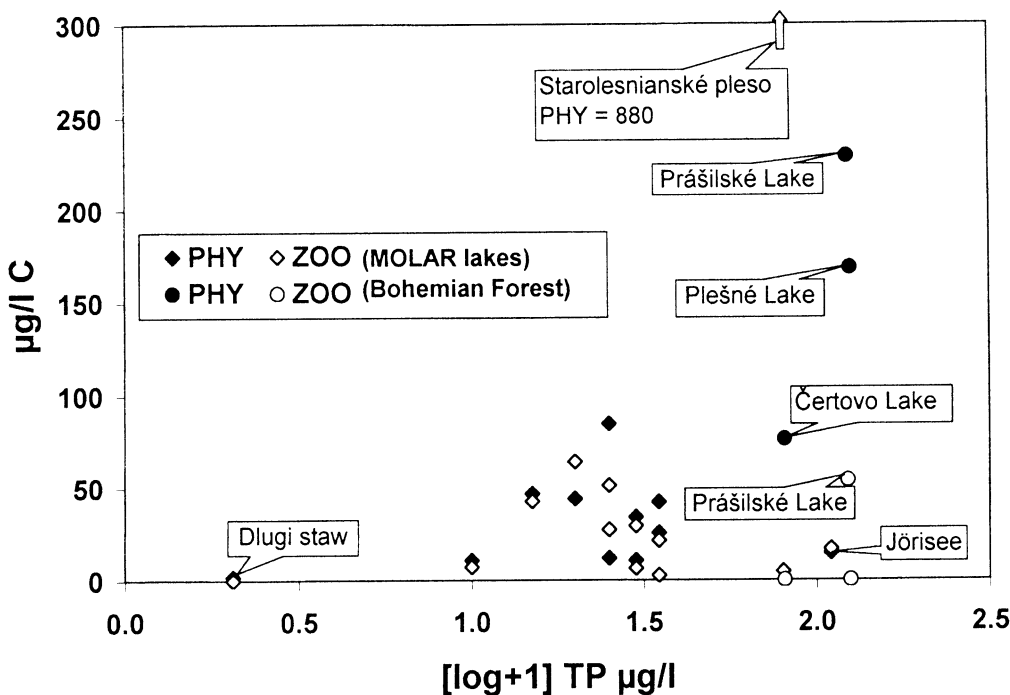


Fig. 2 – Phytoplankton and zooplankton biomass vs. total P, semilog plot, averages.

Forest and in two lakes of Tatra Mts (Starolesnianské pleso and Długi Staw), which are acidified, with the average pH in surface layer below 5.6 (see Table 1). However, in lake Lochnagar (Scotland) with pH 5.3, zooplankton was rather abundant.

We found a remarkably low abundance of all grazers (compared either to total biomass or to the biomass of their prey) in the acidified lakes of Bohemian Forest and Tatra Mts. Both the heterotrophic protozoans (HNF and CIL) were low compared to bacteria (biomass ratios below 0.008, except of Starolesnianské pleso with the ratio 0.6), and zooplankton to phytoplankton biomass ratios were below 0.01, also with one exception (Prášilské lake with the ratio 0.2).

Zooplankton to phytoplankton ratios, however, were remarkably lower in all the Bohemian Forest lakes and in all the Tatra lakes, than in the others, irrespective of pH and total P concentration. In Bohemian Forest and Tatra lakes, at the pH range of 4.8 – 6.5 and total P range of 0.05 to 12.5 $\mu\text{g l}^{-1}$, zooplankton to phytoplankton biomass ratios were found to vary between 0.0001 and 0.23. In all the other lakes (pH range 5.3–8.1 and total P range 1 to 11), the ZOO/PHY ratios varied between 0.19 and 4.29.

Primary production was measured in Øvre Neådalsvatn (August 1996, July 1997), Starolesnianské pleso (June and August 1997) and Długi Staw (September 1997). No autotrophic picoplankton nor filamentous bacteria were found during the dates of measurement, so the size separation between phytoplankton and bacteria was quite efficient. In the lakes of Bohemian Forest primary production was measured frequently during ice-free seasons of 1997 and 1998, but filamentous bacteria were always rather abundant (forming 60 to 70% of bacterial carbon biomass at the average), so the exudates taken up by bacteria could not be determined.

In the former three lakes, the total primary production (average per water column) covered a range of 0.2–11 $\mu\text{g l}^{-1} \text{h}^{-1} \text{C}$ and the percentage of exudation in total primary production was found to be indirectly proportional to total primary production (Fig. 3). Data from similar measurements in a lowland eutrophic reservoir Římov (total production range 8 – 20 $\mu\text{g l}^{-1} \text{h}^{-1} \text{C}$) are included for comparison. In the alpine lakes, the percentage of exudation was between 20 to 90% whereas it was only 8 to 35 % in the reservoir. During 2 h of exposition, 10 to 46 % of exudated C were incorporated by bacteria.

In the three lakes of Bohemian Forest, the averages of total primary production (per column and per seasons) were found in the range 1 – 3 $\mu\text{g l}^{-1} \text{h}^{-1} \text{C}$. Dissolved labelled organic C was 15 to 20% of total production. If we suppose similar percentual uptake by bacteria as in the former lakes, the percentage of exudation would be 22 to 35%.

Discussion

In a large set of data from the lakes of Tatra Mountains (both Slovak and Polish), KOPÁČEK & al. (2000) showed that there is a significant correlation between bacterial numbers and total phosphorus concentration and between chlorophyll and total P in individual samples collected during two years in the autumn from surface layers. However, chlorophyll concentrations were also affected by pH, showing a minimum in the pH range of 4 to 5, and higher chlorophyll values in lakes below pH 4 (such lakes were usually humic ones and they were not included in the survey presented here). Zooplankton in Tatra Mts lakes was not correlat-

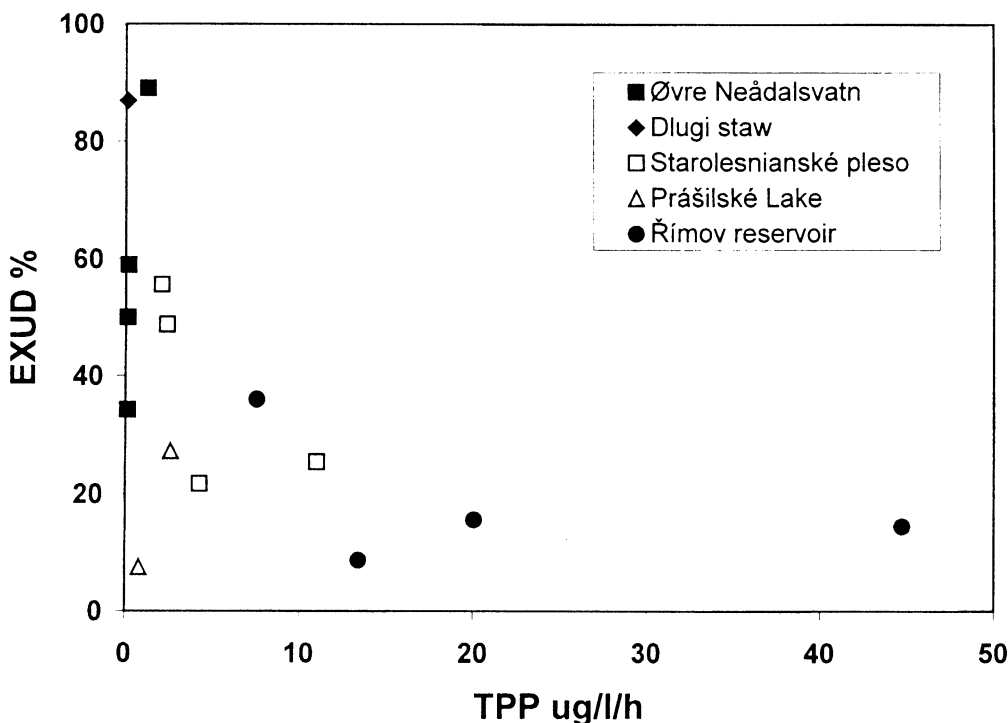


Fig. 3 – Percentage of exudation plotted versus total (gross) primary production in Římov Reservoir and mountain lakes, individual measurements, averages per water column (euphotic part).

ed in the former study, because of a scarce zooplankton abundance and the lack of quantitative data on its biomass.

The scarcity of pelagic crustaceans both in the lakes of Tatra Mts and of Bohemian Forest seems to be connected with an increased concentration of aluminium (especially reactive Al) at low pH. The data on reactive Al are not available from all the other lakes.

Bacteria composed 21 to 90% of total pelagic biomass in 10 out of 15 lakes studied, and less than 10% in 2 of the lakes. In meso- to eutrophic reservoirs the share of bacteria was found to reach 4.5 to 21.8 % in 6 annual averages and varied from 1 to 19.8 in 10 samplings during ice-free seasons. In various meso- to eutrophic lakes it reached 1 to 5% (STRAŠKRABOVÁ & KOMÁRKOVÁ 1979, STRAŠKRABOVÁ & al. 1999b). Compared to this, it could be summarized that the percentual share of bacteria in the total biomass is significantly higher in oligotrophic and ultraoligotrophic clear water lakes than in the lakes of higher trophity. On the other hand, in oligo- to mesotrophic humic lakes the percentual share of heterotrophic protists might be considerable (sometimes surpassing the biomass of phytoplankton) and bacteria reached up to 10%, but only in cases where metazooplankton is not developed. After the development of filtering zooplankton, the biomass of protists and phytoplankton dropped considerably and bacteria may reach more than 80% (KESKITALO & ELORANTA 1999).

Correlation between total pelagic biomass (or phytoplankton biomass) with total phosphorus suggested that not only primary producers and metazoic grazers, but also decomposers are probably phosphorus limited. The only exception – Jörisee III, is the lake with a turbid inflow from glacier. Here a light limitation of primary production might occur, and/or the phosphorus is not readily available due to adsorption to mineral particles.

The correlation between biomass and phosphorus seems not to be affected by differences in total organic carbon concentrations as we could expect, since the heterotrophic biomass could also use allochthonous organic carbon. In the alpine lakes studied, total organic carbon varied from 0.4 to 2.3 and in the lakes from forested catchment it was up to 5.2. Yet, the maximum total pelagic biomass and maximum phytoplankton biomass were reached in Starolesnianské pleso with the average TOC 1 mg l⁻¹ and TP 8 µg l⁻¹, and 3 to 4 times lower biomasses occurred in the lakes in forested catchment at a higher TOC 2.9 – 5.2 mg l⁻¹ and TP 8.1 to 12.5 µg l⁻¹.

A possible explanation might be the high percentual exudation of primary producers. The exudates are readily used by bacteria and most probably they are a preferred substrate compared to the allochthonous carbon. Though the values of total primary production found in mountain lakes were ten times (or more) lower than in lowland, the percentage of extracellular release is considerably higher and bacteria can use exudates as an energy source. Since bacteria are known to sequester phosphorus at very low concentrations more effectively than phytoplankton, they can grow on exudates and then serve as P source for phagotrophic mixotrophs like *Dinobryon*. Primary production and connected bacterial processes apparently are of considerable importance in pelagic region of mountain lakes during ice-free season and bacterial biomass and activity should be considered as important, though some bacterial processes surely are limited by low temperature.

Conclusions

In oligotrophic mountain lakes with low or moderate alkalinity, bacteria and phytoplankton are the major components of pelagic biomass. The share of metazoic plankton is very low especially in the lakes of Tatra Mt and of Bohemian Forest. In these lakes, bacteria reached 40 to 89% of total pelagic biomass.

Heterotrophic protozoan grazers are not numerous even in lakes without metazoic plankton.

Both the phytoplankton and the total pelagic biomass (expressed as carbon) is directly proportional to total phosphorus concentration in clear (not turbid) lakes. The lakes are phosphorus limited similarly in alpine and forested catchments.

Total primary production is by one to two orders of magnitude lower than in the meso- and eutrophic lowland lakes. However, a remarkable percentual extracellular release was observed in most oligotrophic lakes: 40 to 90%. Exudates were immediately used by pelagic bacteria.

There are still some questions remaining:

Why is the abundance of heterotrophic protozoan grazers low in acidified lakes where the filtering metazoic zooplankton is scarce? Is it due to competition with mixotrophic flagellates?

What is the importance of phytoplankton exudates as a source for pelagic bacterial production compared to organic loading from the catchment? Is the allochthonous organic source in alpine lakes really not significant?

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